

Epimyrma adlerzi sp. n. (Hymenoptera: Formicidae) from Greece: morphology and life history

PER DOUWES, KARLA JESSEN and ALFRED BUSCHINGER

Ent. scand.



Douwes, P., Jessen, K. & Buschinger, A.: *Epimyrma adlerzi* sp. n. (Hymenoptera: Formicidae) from Greece: morphology and life history. *Ent. scand.* 19:239–249. Copenhagen, Denmark 28 September 1988. ISSN 0013–8711.

Epimyrma adlerzi is described from material from S, C and N Greece. Morphologically, it is very similar to *E. ravouxi*, a slavemaking species, whereas the biology of *E. adlerzi* is almost identical to that of *E. corsica*. Both are workerless parasites on *Leptothorax exilis*, and have a female biased sex ratio and intranidal mating. Like all other *Epimyrma* species thus far studied the *E. adlerzi* ♀, after having penetrated into a host nest, kills the queen of this colony through protracted throttling with her mandibles. Despite the biological similarities between *E. adlerzi* and *E. corsica* we suggest an independent evolution of workerlessness in these two species. The karyotype of *E. adlerzi* is the same as in its congeners and *Myrmoxenus gordiagini* ($n = 10$).

P. Douwes, Department of Zoology, University of Lund, Helgonavägen 3, S-223 62 Lund, Sweden.

K. Jessen and A. Buschinger, Institut für Zoologie, Technische Hochschule, Schnittpahstr. 3, D-6100 Darmstadt, FRG.

INTRODUCTION

The genus *Epimyrma* Emery, 1915, which is apparently restricted to the SW part of the Palearctic region, includes 7–9 species that are social parasites on members of the subgenera *Myrafant* Smith, 1950 and *Temnothorax* Mayr, 1861 of the genus *Leptothorax* Mayr, 1855 (Buschinger et al. 1986, Espadaler 1982, Kutter 1973). Two species, *E. africana* Bernard, 1948 (assumed to be synonymous with *Leptothorax angulatus* Mayr, 1862 by Kutter (1973)) from N Africa and *E. tamarae* Arnoldi, 1968 from Georgia, USSR are poorly known (only workers described). *E. algeriana* Cagniant, 1968 from N Africa, *E. bernardi* Espadaler, 1982 from Spain, *E. ravouxi* (André, 1896) from C and S Europe, *E. stumperi* Kutter, 1950 from the Alps, and *E. zaleskyi* Sadil, 1953 from Czechoslovakia have workers and are known or assumed to be slavemakers (Buschinger 1982, 1985, Buschinger et al. 1986, Cagniant 1968, Espadaler 1982, Jessen 1987, Kutter 1951, Sadil 1953, Winter 1979). *E. krausseii* Emery, 1915 from S Europe, N Africa and Turkey also has workers, reduced in numbers though and in some popula-

tions almost absent (Buschinger & Winter 1983, Buschinger et al. 1986, Heinze 1987). The remaining species, *E. corsica* (Emery, 1895) from Corsica, C Italy (Mei in litt.) and N Yugoslavia, has no workers (Buschinger & Winter 1985).

Like other social parasites the *Epimyrma* species are more or less host specific. Thus, *algeriana* is living with *L. (M.) spinosus* Forel, 1894 and related species, *bernardi* with *L. (M.) gredosi* Espadaler & Collingwood, 1982, *corsica* with *L. (M.) exilis* Emery, 1869, *krausseii* with *L. (T.) recedens* (Nylander, 1856), *ravouxi* with *L. (M.) unifasciatus* (Latreille, 1798) and *L. (M.) nigriceps* Mayr, 1855 (and also with *L. (M.) affinis* Mayr, 1855 (Winter, Faber & Buschinger unpubl. obs.)), *stumperi* with *L. (M.) tuberosum* (Fabricius, 1775), and *zaleskyi* with *L. (M.) affinis* (Buschinger 1982, Buschinger & Winter 1983, Buschinger et al. 1986, Cagniant 1968, Espadaler 1982, Kutter 1973, Sadil 1953).

Until recently hardly any records of *Epimyrma* existed from SE Europe. In the years 1978–1985 we collected a workerless *Epimyrma* species in different parts of Greece (Fig. 1). A total of 10 *L.*

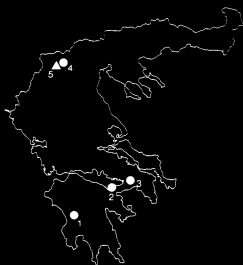


Fig. 1. Distribution of *Epimyrma adlerzi* sp. n. (●) and *E. ravouxi* (André) (▲) in Greece. 1 = Bassai, S Andritseni; 2 = Blue Lake, W Loutraki; 3 = Kaza, S Thivae; 4 = Klidion, S Florina; and 5 = Drosopigi, S Florina.

(*M.*) *exilis* colonies were found containing this undescribed *Epimyrma* species.

MATERIALS AND METHODS

All colonies of *Leptothorax (M.) exilis* with *Epimyrma* were collected and 7 of them brought alive to the laboratory for biological studies. These colonies and a total of 19 successfully founded in the laboratory were kept under artificial conditions as described by Buschinger (1974) and Buschinger et al. (1986). Since we are lacking exact climatic data from the localities where we found *E. adlerzi*, we chose a temperature regime which had proved suitable already for several Mediterranean *Epimyrma* and *Chalepoxenus* species. Thus for hibernation the colonies were kept in nearly constant 10°C for 3–5 months, then placed in a 12:12 hours rhythm of 10°C, dark/20°C, light for 2 weeks, and in a rhythm of 15°C (10h, dark) to 25°C (14h, light) for another 2 weeks, finally in 17°C (10h, dark) to 28°C (14h, light) for about 2 months or until pupation of brood decreased. Through the 15/25°C and the 10/20°C rhythms, as in "spring", the colonies then were brought into a second hibernation. Honey diluted with water, and insect pieces (cockroaches, *Tenebrio* pupae)

were supplied ad libitum three times a week.

The karyotype of *E. adlerzi* was determined using the method of Imai et al. (1977). We analyzed the testes of 4♂-pupae from colonies of Bassai, Blue Lake and Klidion. From each pupa 20 metaphase plates were checked for chromosome number and shape. The morphological study was based on field collected material from 3 colonies from Blue Lake (N in Fig. 4 and Table 1) and laboratory bred individuals from 5 colonies. For comparison we examined also material of the other *Epimyrma* species occurring in the Mediterranean area, i.e. *algeriana*, *bernardi*, *corsica*, *kraussei*, and *ravouxi* (Fig. 4).

Alitrunk length was measured from the vertical slope of pronotum to the posteriormost tip of propodeum. All measurements (in mm unless otherwise stated) given in the description (mean \pm 1 standard deviation) are based on the field collected material, since we suspect size to be influenced by laboratory conditions. For the morphology of the genus *Epimyrma*, see Kutter (1973).

TAXONOMY

Epimyrma adlerzi sp. n.

(Figs. 2–5)

Type locality: Greece, Korinthos, Blue Lake W Loutraki.

Type material: Holotype ♀, Greece: Blue Lake W Loutraki, 17.x.1984, P. Douwes. — *Paratypes*: Greece: 9♀ 1♂, same data as for holotype; 1♀ 1♂, same locality as for holotype, 24.ix.1978, P. Douwes; 3♂♂, same locality as for holotype, 4.x.1985, Buschinger-Douwes-Heinze-Jessen-Winter, Laboratory stock S Nr Je 24d; 7♀ 1♂, same locality as for holotype, 4.x.1985, Buschinger-Douwes-Heinze-Jessen-Winter, Laboratory stock S Nr 12296; 5♀ 2♂♂, Thivae, Kaza, 8.x.1985, Buschinger-Douwes-Heinze-Jessen-Winter, Laboratory stock S Nr 12326; 3♀ 7♂♂, Florina, Klidion, 9.x.1985, Buschinger-Douwes-Heinze-Jessen-Winter, Laboratory stock S Nr 12347.

The holotype and 12 paratypes are in Museum of Zoology, Univ. of Lund, Sweden; 15 paratypes in Zoologische Staatssammlung, Munich, FRG; 6 paratypes in Naturhistorisches Museum, Basel, Switzerland; 7 paratypes in British Museum (Nat. Hist.), London, UK; and 7 paratypes in Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA.

Etymology: Named in honour of the Swedish myrmecologist Gottfrid Adlerz.

Diagnosis: *E. adlerzi* is in colour and sculpture almost identical with *ravouxi*. Despite the fact that the petiolus form is highly variable in *Epimyrma* species, as pointed out by Kutter (1973) and confirmed in this study, the ventral lobe in profile and the angle between the anterior and posterior faces of the node offer the best discrimination between *adlerzi* and *ravouxi* females (Figs. 3, 4). There are also slight differences in the petiolus height/alitrunk length, postpetiolus height/alitrunk length, and head length/alitrunk length ratios (Fig. 4). Size varies considerably in *ravouxi*, southern populations having more or less the same alitrunk length as *adlerzi*. It should be remembered, however, that all but one sample of *adlerzi* consist of laboratory bred individuals which seem to be larger than normal (cf. the two samples from Blue Lake, Fig. 4). The four species *adlerzi*, *algeriana*, *bernardi*, and *ravouxi* show great similarities in the male genitalia with cuspis reaching and usually overlapping digitus (Fig. 5), and in the sculpture of the female which is punctuated rather than longitudinally striate. The sculpture is very poorly developed in *bernardi*, however, which appears smooth and shining all over the body. This species is also characterized by the large postpetiolus width/length ratio in the female (Fig. 4). *E. algeriana* differs from *adlerzi* mainly in sculpture (most of ep1 and lateral parts of pronotum are smooth) and the more pointed petiolus angle in the female (Fig. 4). In morphology *E. adlerzi* shows least similarity to *corsica* which is also workerless and which has the same host species. *E. corsica* is on average smaller and darker, has a flatter alitrunk, and is smoother and more shining due to less pronounced punctation. The characteristic ventral petiolus projection in the *corsica* male is totally absent in *adlerzi*. Male genitalia differ too, the digitus being relatively thicker in *corsica*. *E. kraussei* has about the same weak sculpture as *corsica* and, furthermore, *kraussei* males have a ventral projection on petiolus, though less pronounced than in *corsica*. In the male genitalia of *kraussei* cuspis does not reach digitus. Although there seems to be little differentiation in pilosity between the species, *kraussei* is distinctly more hairy than *adlerzi* and probably all other *Epimyrma* species, cf. Kutter (1973).

Description

Female (Figs. 2-4)

Head. Brown, frons, vertex and antennal club dark brown. Punctuated with faint (strong on occiput) more or less longitudinal ridges. Clypeus and mandibles smooth. Clypeus with median and lateral ridges, median one not reaching posterior margin. Hairs (max. length 0.1) erect all over except adpressed on the antennae. Length = 0.59 ± 0.02 . Width (incl. eyes) = 0.55 ± 0.02 .

Alitrunk (= thorax + propodeum). Pale brown usually with irregular darker markings laterally and characteristic dark markings along anterior margin of mesonotum and a longitudinal spot on each side. Scutellum at least partly dark brown.

Sometimes whole alitrunk dark brown with indistinct markings. Punctuated except on median part of scutellum, lower part of ep1, and whole of ep2 which are smooth (Fig. 2). Longitudinal ridges on mesonotum, lateral parts of scutellum, posterior part of ep2, and lateral parts of propodeum. Transverse ridges on posterior face of propodeum. Erect hairs (max. length 0.1) especially on pro- and mesonotum. Adpressed hairs on legs except erect on coxae and trochanters. Length = 0.87 ± 0.03 . Width = 0.49 ± 0.02 .

Pedicel. Pale brown. Petiolus and postpetiolus nodes faintly punctuated, the ventral parts smooth. Angle between anterior and posterior faces of petiolus is $48 \pm 4^\circ$ (Fig. 3). In side view, posteroventral part of petiolus forms a convex or sometimes partly straight (but never concave) line (Fig. 3). Erect hairs on petiolus and postpetiolus nodes (max. length 0.16 on postpetiolus). Petiolus height = 0.36 ± 0.01 , width = 0.17 ± 0.01 . Postpetiolus height = 0.28 ± 0.02 , width = 0.25 ± 0.01 .

Gaster. Smooth and dark brown, first tergite usually pale brown at base. Abundant erect hairs.

Male (Figs. 2, 5, Table 1)

Head. Black, antennae pale, greyish brown, mandibles pale yellowish brown. Punctuated, longitudinal ridges on occiput. Mandibles, median part of clypeus, and median stripe of frons smooth. Clypeus with median and lateral ridges, median one not reaching posterior margin. Erect hairs (max. length 0.1) all over, the antennae with dense erect pilosity. Length = 0.50 ± 0.01 . Width (incl. eyes) = 0.52 ± 0.01 .

Alitrunk. Black, sometimes partly very dark brown. Punctuated except on median part of scutellum and ep2 (Fig. 2). Faint transverse ridges on posterior face of propodeum. Erect hairs (max. length 0.1) especially dorsally. Legs pale greyish brown with adpressed hairs (erect on coxae and trochanters). Length = 0.94 ± 0.01 . Width = 0.48 ± 0.01 .

Pedicel. Black, faintly punctuated. Erect hairs, longest on postpetiolus (max. length 0.14). Petiolus height = 0.24 ± 0.01 , width = 0.15 ± 0.00 . Postpetiolus height = 0.24 ± 0.00 , width = 0.24 ± 0.01 .

Gaster. Black and smooth. Abundant erect hairs. Cuspis overlaps digitus.

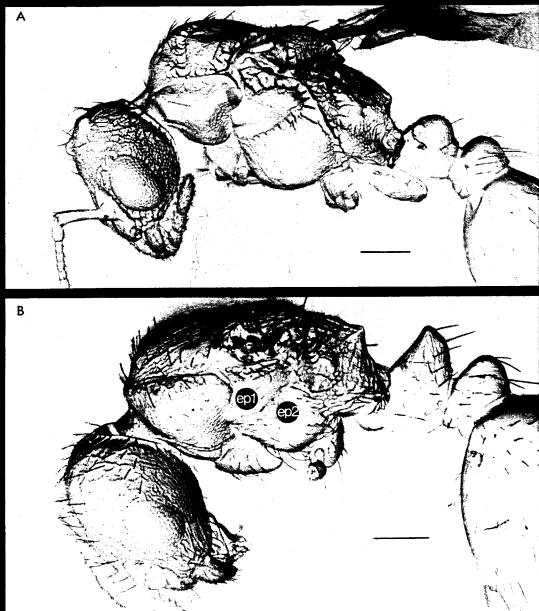
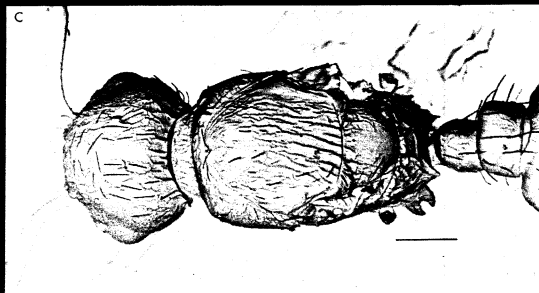


Fig. 2. SEM micrographs of *Epimyrma adlerzi* sp. n.: A = male (Bassai), lateral view; B = female (Blue Lake, Je 24f), lateral view; C = female (Blue Lake, Je 24f), dorsal view. Scale = 0.2 mm; ep1 and ep2 = mesopleurae.

Karyotype

The karyotype of *E. adlerzi* is identical, and presumably homologous, with those of all other *Epimyrma* species yet studied (*kraussei*, *bernardi*, *ravouxii*, *stumperi*, *algeriana*) and with that of

Myrmoxenus gordiagini. It comprises a haploid number of 10 chromosomes, of which 6 are medium-sized and metacentric, 3 are medium-sized and submetacentric, and 1 is large and subtelocentric (Fig. 6).



LIFE HISTORY

Worker number

In none of the 10 field collected colonies of *Epimyrmica adlerzi* any worker had been found. In a total of 24 laboratory culture colonies, of which some were maintained for two breeding seasons, a total offspring of 745 females were obtained. Only one of these, descended from a colony collected at Bassai, was a worker, all others were alate females. We therefore conclude that *E. adlerzi* is a workerless species.

Host species

All the 10 field collected colonies had workers of *Leptothorax exilis* as host species. This species was also frequent at the collecting sites, and our laboratory experiments on *E. adlerzi* colony foundation were carried out with this species.

Sexual behaviour

We never saw alates of *E. adlerzi* outside their nests, except for males who sometimes leave the nest just a few hours before they die. Mating occurs within the mother nest, among siblings, as in some other *Epimyrmica* species which we have studied during the past years (*E. kraussae*, *corsica*, *bernardi*, *algeriana*).

Mating attempts can often be seen when an artificial nest with alates is uncovered and exposed to light, but mating occurs also when the colonies are observed in damp red light. Dealate females taken out of the nests are usually inseminated. On 27 October 1985, we could observe the complete mating behavior in one of the colonies collected in 1984.

Three dealate and two alate females, and one male were present in the nest which was kept in an incubator. Between 9.00 and 11.00, after the

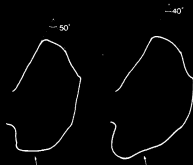


Fig. 3. Petiolus in profile of *Epimyrmica adlerzi* sp. n. (left) and *E. ravouxi* (André) (right) females, showing the petiolus angle and the outline of the ventral projection (lamella).

		No. colonies and individuals	ALIT L (mm)			ALIT W/L		PET H/ALIT L		PPET H/ALIT L		HEAD L/ALIT L		
			0.8	0.9	1.0	0.55	0.60	0.40	0.45	0.30	0.35	0.65	0.70	
<u>ADLERZI</u>														
Bassai	1	5		●			●		●		●		●	
Blue Lake (N)	3	11	●	●			●		●		●		●	
— — —	1	10		●			●		●		●		●	
Kaza	1	5		●			●		●		●		●	
Klidion	1	3		●			●		●		●		●	
<u>RAVOUXI</u>														
Drosopigi	2	13		●			●		●		●		●	
Corsica	2	15		●			●		●		●		●	
Nyons	1	4		●			●		●		●		●	
Neubrück	1	6		●			●		●		●		●	
Tauber valley	2	10		●			●		●		●		●	
<u>ALGERIANA</u>														
F. de Yakouren	2	7	●	●			●		●		●		●	
<u>BERNARDI</u>														
S. de Gredos	1	2		●			●		●		●		●	

		PET W/H		PPET W/H		HEAD W/L		PET ANGLE		% CONV. PET			
		0.45	0.55	0.9	1.0	0.9	1.0	40	50	60	0	50	100
<u>ADLERZI</u>													
Bassai	1	5	●	●		●		●	●				●
Blue Lake (N)	3	11	●	●		●		●	●				●
— — —	1	10		●		●		●	●				●
Kaza	1	5	●	●		●		●	●				●
Klidion	1	3	●	●		●		●	●				●
<u>RAVOUXI</u>													
Drosopigi	2	13	●	●		●		●	●		●		●
Corsica	2	15		●		●		●	●		●		●
Nyons	1	4	●	●		●		●	●		●		●
Neubrück	1	6	●	●		●		●	●		●		●
Tauber valley	2	10	●	●		●		●	●		●		●
<u>ALGERIANA</u>													
F. de Yakouren	2	7		●		●		●	●				●
<u>BERNARDI</u>													
S. de Gredos	1	2		●			●	●	●		●		●

Fig. 4. Body measurements of samples of *Epimyrmica adlerzi* sp. n., *E. ravouxi* (André), *E. algeriana* Cagniant, and *E. bernardi* Espadaler females. ALIT = alitrunk; PET = petiolus; PPET = postpetiolus; H = height; L = length; W = width; N = individuals collected in the field. For petiolus angle and convexity of petiolus see Fig. 3. Mean \pm 1 standard deviation is shown. % conv. pet. = percentage of specimens with convex outline of petiolar lamella.

Sample	No. ind.	Alit L	Alit W/L	Pet H/Alit L	Ppet H/Alit L	Head L/Alit L	Pet W/H	Ppet W/H	Head W/L
Blue Lake (N)	2	0.94±0.01	0.51±0.01	0.25±0.01	0.26±0.00	0.54±0.02	0.64±0.04	0.98±0.06	1.03±0.01
S Greece	8	1.02±0.03	0.59±0.02	0.28±0.01	0.26±0.01	0.53±0.01	0.62±0.03	0.96±0.05	1.06±0.03
N Greece	5	1.08±0.02	0.55±0.01	0.25±0.01	0.24±0.01	0.51±0.01	0.65±0.02	1.01±0.03	1.09±0.01

Table 1. *Epimyrma adlerzi* sp. n. Body measurements of males (mean \pm 1 standard deviation). Alitrunk length is given in mm. Individuals from S Greece are from Bassai, Blue Lake and Kaza, from N Greece from Klidion. Alit = alitrunk, Pet = petiolus, Ppet = postpetiolus, H = height, L = length, W = width, N = individuals collected in the field.

morning raise in temperature from 17°C to 28°C at 6.00, continuous mounting attempts of the male were seen. At 11.00, as one of the alate females shed off her wings, the male was trying to mate with the remaining alate female. Half an hour later the male was still sitting on top of the female, vigorously palpating her head and neck with the antennae and keeping her wings between his legs. Once the extruded genitalia of the male were licked by a host worker. The male grasped the female's thorax with his forelegs, and continuously dabbed the female's gaster with his genitalia, mostly from below. At 11.45, after at least 45 minutes of "courtship", the male suddenly inserted his genitalia into the female's cloaca. The mating itself lasted only 10 seconds. During this time the male bent backwards releasing his grip around the female's thorax and wings. The female, in this position, had her stinger extruded and kept upright in nearly a right angle to her body. We have observed this behaviour also in *Epimyrma*

kraussei, *Chalepoxenus* spp. and *Harpagoxenus sublaevis* (Nylander, 1849).

Only one minute after copulation the female began breaking off her wings, and after 5 min. only one hind wing was still left in place. The male tried to mount the female again, but she crouched and retracted all appendages until the male gave up.

Colony foundation behavior

In *Epimyrma kraussei* and *E. corsica*, the mated and dealate females remain in their mother nests over winter. In early spring they leave on foot in search for new host colonies, into which they then penetrate in attempts to found their own colonies after killing and replacing the host's queen (Buschinger & Winter 1985, Buschinger et al. 1986). *Epimyrma adlerzi* females can apparently exhibit a similar behavior, since all the four colonies collected at Loutraki in October 1984 and 1985 still contained several dealate females. In the remaining three colonies (Table 2), only the queen was present when the nests were found. Any offspring of young females either had already left these nests, or the colonies were newly founded. In either case, colony foundation must have occurred prior to hibernation in the populations from

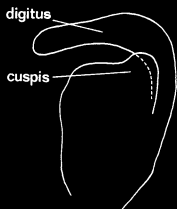


Fig. 5. Volsella and lacinia of *Epimyrma adlerzi* sp. n.

Table 2. The original composition of the 5 *Epimyrma adlerzi* sp. n. colonies collected in October 1985.

Locality	<i>E. adlerzi</i>			<i>L. exilis</i>		
	♀ ♀ ¹	♂ ♂	♀ ♀	♀ ♀	Eggs ²	Larvae ²
Blue Lake 3	—	—	10	1	—	4
Blue Lake 9	8	—	38	6	—	2
Bassai 1	—	—	104	7	—	5
Kaza 1	—	—	31	—	—	5
Klidion 1	—	—	48	—	—	2

¹ dealate ² presumably of *E. adlerzi*.



Fig. 6. Karyotype of *Epimyrma adlerzi* sp. n.

which these three colonies were taken. Thus, *E. adlerzi* is perhaps more flexible than the other nest-mating *Epimyrma* species, with respect to the season of colony foundation. Presumably this is correlated with different climatic conditions in the various areas of distribution. Laboratory experiments were conducted with material from the Loutraki population, in early spring 1986, after the females had spent the winter in their mother nests. Several females were observed to leave the nests already during the artificial hibernation, in temperatures of 8–10° (their offspring, one year later, exhibited the same behavior). Females were removed when they spontaneously had left the nests, crawling around in the food and water chambers of the formicaries. They were then placed into parts of formicaries inhabited by complete (queenright) host species colonies of various sizes.

The results of the female transplant experiments revealed that females of *E. adlerzi* exhibit nearly the same colony foundation behaviour as we had observed in other *Epimyrma* species. The *E. adlerzi* female, often shortly after having been placed in the host species formicary, enters the nest, and if not seized by the host species workers and evicted, she soon locates the host colony queen and begins to throttle her with the mandibles around her neck or throat (Fig. 7). During this throttling, which often lasts for hours and may be repeated during up to three weeks, the *Epimyrma* female frequently brushes with her forelegs over the head and thorax of her victim, and

then, with curiously contorted legs, over her own body. She interrupts the throttling frequently and licks the mouthparts or the surface of the host queen which is sometimes paralyzed already after half an hour of throttling. Now and then she also solicits food from the host workers which appear surprisingly unaffected of what happens to their queen. The host queen is usually kept paralyzed for about two weeks (once 4 weeks) until she finally dies and is carried out of the nest. During colony foundation, the *Epimyrma* female sometimes stings one or a few host workers which may either die after 2 or 3 days, or recover. However, in *E. adlerzi* we saw this behavior much rarer than, e.g. in *E. kraussei* (Winter & Buschinger 1983). In order to give an impression of the colony founding process, we present extracts of an experiment which should represent what we believe is a "normal" colony foundation, with as little experimental manipulation as any possible:

4 Feb. 1986

13.20

E. adlerzi ♀ put into formicary with queenright *L. exilis* colony of ca. 30 ♀♀. The *E.a.* colony had been brought from hibernation (10°C) into "spring conditions" (10°/20°C) on 03.02.86. Observations under laboratory conditions (ca. 22°C, light). The *L.e.* colony is outside the nest, in the food chamber of the formicary.

13.24

E.a. ♀ begins alternately to throttle *L.e.* ♀, and to lick and palpate the head, pedicel and gaster of *L.e.* ♀. The *L.e.* ♀ vigorously tries to escape her grip.



Fig. 7. Colony foundation of *Epimyrma adlerzi* sp. n. The parasite ♀ (right, smaller) throttles the queen of *Leptothorax exilis* Emery by seizing her neck with the mandibles, amidst the workers and brood of the host species colony. Photo: W. Ehrhardt.

until 13.52

Repeated throttling, brushing, palpating, licking mouthparts of *L.e.* ♀. *L.e.* ♀ lying on her back, paralyzed.

13.55

E.a. ♀ throttles, apparently with all her energy, *L.e.* ♀ bends her body convulsively. *E.a.* ♀ brushes.

until 17.21

E.a. ♀ alternately throttles and brushes *L.e.* ♀, and brushes herself with the forelegs, then licks *L.e.* ♀ mainly on her mouthparts and tip of the gaster, sometimes the *E.a.* ♀ solicits food from *L.e.* ♀ ♀ (usually after having licked the *L.e.* ♀'s mouthparts – received some substance there which attracts the ♀ ♀?). Colony placed in 10°/20°C incubator.

until 6 Feb. 1986

Observations of throttling, licking, brushing, food exchange with ♀ ♀ continued.

11.30

Colony has moved into the nest, together with the host and parasite females.

until 12 Feb. 1986

E.a. ♀ continued throttling, licking etc., now sitting on top of the brood. The *L.e.* ♀ lies on her back, beside the colony, moving her legs only weakly. Her mouthparts are protruded and seem incrustated by some secretion.

13 Feb. 1986

11.55

L.e. ♀ is dragged out of the nest by *L.e.* ♀ ♀, has lost an antenna, but still moves her legs a little.

14 Feb. 1986

E.a. ♀ becoming physogastric, sitting on the brood. *L.e.* ♀ dead.

until June 1986

Production of some *L.e.* ♀ ♀ from the brood.

18 June 1986

First 3 *E.a.* ♀ pupae present.

25 June 1986

5 ♀ pupae, 1 ♂ pupa.

until 17 Sep. 1986

A total of 45 ♀ ♀ and 8 ♂ ♂ produced.

Sexual production and sex ratio

The production of five of the field-collected colonies in the first and second season after collecting, and of 19 colonies founded in the laboratory, are presented in Table 3. For at least two of the five colonies, the "first" season presumably was the second one, because they already contained a few

Table 3. Brood production and sex ratio of *Epimyrma adlerzi* sp. n. colonies.

	No. of: ♀ ♀	(mean)	♂ ♂	(mean)	♀ ♀	Sex ratio ♂/♀	No. of colonies
Coll. in the field							
1st season	116	(23.2)	27	(5.4)	1	0.233	5
2nd season	39	(9.8)	13	(3.3)	—	0.333	4
Founded in the lab.							
1st season	464	(24.4)	86	(4.5)	—	0.185	19
2nd season	125	(17.9)	16	(2.3)	—	0.128	7

sexuals when collected in October 1985. The number of colonies from which we obtained a second brood was lower than that of the first season, because some colonies or their queens died before or during the first hibernation. The sex ratio (142 ♂♂ : 744 ♀♀) is 0.191 and thus strongly female biased, as is usual in inbreeding species, and similar to sex ratios that we found in other nest-mating *Epimyrma* species (*E. kraussei*: 0.3, Winter & Buschinger 1983; *E. corsica*: 0.083, Buschinger & Winter 1985).

Most of the sexual production in *E. adlerzi* is due to "rapid brood" developing from the egg to the adult instar within one summer (and fall) season, as may be seen from the laboratory-founded colonies in Table 3. We also observed that during hibernation only very few eggs and larvae were present in the nests (Table 2). Thus, the second brood should also consist mainly of specimens having developed from eggs laid in the second season.

The few sexuals present in the field colonies when we collected them (Table 2) are in contrast to the high numbers produced in the laboratory cultures. Presumably, in the field colonies some females had already left the nests and some males had died before the collecting. Nevertheless, we assume that in the laboratory, with constant food supply and apparently adequate temperature and humidity conditions, we attained a higher sexual production than is usually achieved in the field. The bigger size of laboratory-reared as compared to field specimens may be another evidence for "too good" laboratory conditions.

E. adlerzi queens often died already in the year of their colony foundation. Others did not survive the second year, and a third brood production was only exceptionally possible, also because the host workers rarely survive such long. The life

expectancy of *E. adlerzi*, thus, is certainly not much more than two years, as in *E. corsica* and *E. kraussei*. On the contrary, we estimated a life expectancy of up to 10 years for the worker-producing and slave-raiding *E. ravouxi* (Buschinger & Winter 1983).

DISCUSSION

Epimyrma apparently represents a monophyletic group of species (perhaps including also *Myrmoxenus gordiagini* (Buschinger et al. 1983)). Within this group an evolutionary progression is evident, beginning with truly dulotic species (*E. ravouxi*, *E. stumperi*, *Myrmoxenus gordiagini*), the sexuals of which also make mating flights. In *E. algeriana* and *E. bernardi*, both still having numerous workers and conducting slave raids (Jessen 1987), a tendency towards mating inside the mother nest has evolved. *E. kraussei* (Buschinger et al. 1986) has reduced the worker numbers and does not or only exceptionally conduct slave raids. Finally, *E. corsica* has proved to be completely workerless (Buschinger & Winter 1985). *E. kraussei* and *E. corsica*, as *E. adlerzi*, also exhibit the feature of sib-mating within the mother nests. All the *Epimyrma* species and *M. gordiagini* have a common, and apparently homologous karyotype of $n = 10$ chromosomes. And all these species share the particular colony foundation behavior of the queens which eliminate the host colony queens by protracted throttling.

E. adlerzi, thus, apparently represents a final stage in the evolutionary sequence within the genus, and in its biology it is remarkably similar to *E. corsica*, the other workerless species of this group. They share the same host species, *L. exilis*, and host specificity is usually high in the "dege-

nerate slavemakers" among the *Epimyrma* species. However, the hosts of *adlerzi* appear brown in coloration, whereas the *exilis* populations infested by *E. corsica*, in Corsica and Yugoslavia, are uniformly black. The two color forms might represent different taxa on the subspecies level. However, Baroni Urbani (1971) has synonymized all the described subspecies and varieties of *exilis* under this species name.

A morphological comparison of *E. adlerzi* with *E. corsica* revealed conspicuous differences, while one of the slavemaking species, *E. ravouxi* is morphologically closely similar to *E. adlerzi*. Thus, we doubt that *E. corsica* is the closest relative of *E. adlerzi* and believe in an independent, convergent loss of workers in the two species.

Acknowledgements — The work was supported by a grant of the Deutsche Forschungsgemeinschaft to A.B. We wish to thank J. Heinze and U. Winter for assistance during collecting the ants.

References

- Baroni Urbani, C. 1971. Studien zur Ameisenfauna Italiens XI. *Revue suisse Zool.* 78: 1037–1067.
- Buschinger, A. 1974. Experimente und Beobachtungen zur Gründung und Entwicklung neuer Sozietäten der sklavenhaltenden Ameise *Harpagoxenus sublaevis* (Nyl.). *Insectes soc.* 21: 381–406.
- 1982. *Epimyrma goesswaldi* Menozzi 1931 = *Epimyrma ravouxi* (André 1896) — Morphologischer und biologischer Nachweis der Synonymie (Hym., Formicidae). *Zool. Anz.* 208: 352–358.
- 1985. New records of rare parasitic ants (Hym., Form.) in the French Alps. *Insectes soc.* 32: 321–324.
- Buschinger, A., Fischer, K., Guthy, H.-P., Jessen, K. & Winter, U. 1986. Biosystematic revision of *Epimyrma kraussei*, *E. vandeli*, and *E. foreli* (Hymenoptera: Formicidae). *Psyche, Camb.* 93: 253–276.
- Buschinger, A. & Winter, U. 1983. Population studies of the dulotic ant, *Epimyrma ravouxi*, and the degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). *Entomologia gen.* 8: 251–266.
- 1985. Life history and male morphology of the workerless parasitic ant *Epimyrma corsica* (Hymenoptera: Formicidae). *Ibid.* 10: 65–75.
- Buschinger, A., Winter, U. & Faber, W. 1983. The biology of *Myrmoxenus gordiagini* Ruzsky, a slave-making ant (Hymenoptera, Formicidae). *Psyche, Camb.* 90: 335–342.
- Cagniant, H. 1968. Description d'*Epimyrma algeriana* (nov. sp.) (Hyménoptères Formicidae Myrmicinae), fourmi parasite. Representation des trois castes. Quelques observations biologiques, écologiques et éthologiques. *Insectes soc.* 15: 157–170.
- Espadaler, X. 1982. *Epimyrma bernardi* n. sp. a new parasitic ant (Hymenoptera, Formicidae). *Spixiana* 5: 1–6.
- Heinze, J. 1987. Three species of social parasitic ants new to Turkey. *Insectes soc.* 34: 65–68.
- Imai, H.T., Crozier, R.H. & Taylor, R.W. 1977. Karyotype evolution in Australian ants. *Chromosoma* 59: 341–393.
- Jessen, K. 1987. Biosystematic revision of the parasitic ant genus *Epimyrma*. In Eder & Rembold, Chemistry and biology of social insects. München.
- Kutter, H. 1973. Beitrag zur Lösung taxonomischer Probleme in der Gattung *Epimyrma* (Hymenoptera Formicidae). *Mitt. schweiz. ent. Ges.* 46: 281–289.
- Sadil, J. 1953. *Epimyrma zaleskyi* nov. spec. *Roč. čsl. Spol. ent.* 50: 188–196.
- Winter, U. 1979. *Epimyrma goesswaldi* Menozzi, eine sklavenhaltende Ameise. *Naturwissenschaften* 66: 581.
- Winter, U. & Buschinger, A. 1983. The reproductive biology of a slavemaker ant, *Epimyrma ravouxi*, and a degenerate slavemaker, *E. kraussei* (Hymenoptera: Formicidae). *Entomologia gen.* 9: 1–15.

Revised manuscript accepted February 1988.